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ROOT DISTRIBUTION AND ENVIRONMENT IN A MAPLE-OAK FOREST

A DISSERTATION SUBMITTED TO THE FACULTY OF THE DIVISION OF THE BIOLOGICAL SCIENCES IN CANDIDACY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
1942

By
NORBERT J. SCULLY

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ROOT DISTRIBUTION AND ENVIRONMENT IN A MAPLE-OAK FOREST

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 537

NORBERT J. SCULLY

(WITH TWENTY-ONE FIGURES)

Introduction

Various studies have emphasized the importance of investigating root distribution (*a*) as a phase of the structure of communities; (*b*) in correlation with horizonal characteristics of soil profiles which might directly or indirectly affect root growth; (*c*) as a background for the logical sampling of soil factors; (*d*) in interpreting plant competition studies and individual plant responses. All these outlooks are necessary in a complete analysis of environment and community relationships. The present study was approached primarily from the first two points of view but also furnishes a background for further work along other lines.

The trench method of investigating roots (18) offers no difficulty when most roots present belong to one or a few dominant species. In deciduous forests with luxuriant ground cover, however, difficulties in root identification tend to limit the value of such study to simple correlation based only on the total root distribution, although many of these difficulties can be overcome by certain modifications and additions to the method.

Investigation of root distribution by the trench method is essentially statistical. Any method employed should measure accurately the variability in the population to be sampled. A refinement of methods to cope with the degree of heterogeneity is desirable. The present investigation offers a partial solution to the problem in deciduous forests, where roots are numerous. Further, it seems desirable that any study of relationship between root distribution and environment should consider the whole biology of the soil profile. Such study demands analysis of the soil proper; of inherent growth tendencies of the root systems of given dominant species as well as their responses to specific soil characters; and—of equal importance in most habitats—the role played by soil invertebrates and burrowing animals. Animal activities are in need of much more study, particularly in regions exhibiting the mull type of forest soil profile.

The present study consists primarily of a root distribution and environment investigation in a 65-acre tract of sugar maple–red oak–white oak forest. Counts were made of all roots occurring in profiles of sixteen selected stations, employing an old and a new method of trench sampling; and an attempt was made to cor-

relate their occurrence in number, size, and area to the respective horizonal features. A number of physical soil factors and the occurrence and role of earthworms and cicada nymphs in the profiles were observed.

The investigation was conducted during the summers of 1938, 1939, and 1940 at Wychwood, Lake Geneva, Walworth County, Wisconsin.

Regional habitat conditions

Climate

Nearly all of Walworth County is included within the Rock River basin. This climatic province has the longest growing season of any in Wisconsin, averaging approximately 170 days (20). The mean annual temperature at the Weather Bureau Station at Delevan, a few miles from Wychwood, is 46.0° F. The average annual precipitation of 31.4 inches is distributed rather uniformly throughout the growing season, with an average rainfall of more than 2.6 inches per month from April to September, inclusive. The data from the Delevan station indicate comparatively slight climatic fluctuation.

Physiography

Wychwood lies on the Darien moraine of the "kettle-range," one of the most striking topographic features of a large portion of eastern Wisconsin (17). About Lake Geneva, on the north shore of which Wychwood is located, the topography is typically irregular. Within the 65 acres of forest a definite knob-and-kettle topography is found, although there are only a few true kettles. Slopes of 15°–20°, occasionally extending 100 feet or more, are comparatively common. The land rises to the north in the $\frac{2}{3}$-mile length to a maximum of 1029 feet above sea level, or 168 feet above the lake, affording good conditions for drainage. A few depressions without surface outlets occur, but they normally possess comparatively good internal drainage.

Soil

All profiles examined at Wychwood correspond to the Bellefontaine silt loam type (8, 11, 17), a characteristic type on the more rolling till deposits in eastern Wisconsin, belonging to the Gray-Brown Podsolic Group. The underlying rock formation, from which the glacial deposits at Wychwood are derived in large part, is Niagara limestone. Owing to the calcareous nature of the parent soil material and the annual return of large supplies of bases to the surface through the decomposition of fallen leaves, a "coarse mull" type (7) of soil has developed in which the organic matter is intimately mixed with the upper few inches of the mineral soil.

The A_0 horizon is variable in thickness because of the irregular local topography

and because the annual leaf fall completely disappears, except for occasional petioles, before the next year's foliage is shed. The rapidity with which leaves decompose in this forest during the summer months is unusual. The possible role of earthworms (*Lumbricus* spp.) in this regard is treated later.

The profiles examined typically had a dark gray, silt loam A_1 horizon with an average depth of 4 inches. With few exceptions, the horizon is relatively high in organic matter in the specific stations and in other sampled areas. Numerous small but visible pores were evident, and the soil was distinctly crumbly and friable.

The A_2 horizon, occasionally absent, was a grayish yellow silt loam, indication that leaching had not been complete. It was somewhat lighter in texture than the A_1. Encountered at an average depth of 4 inches, it had an average thickness of 5 inches. Typically this horizon was the lightest colored in the profile and showed a slight blocky structure at its lower levels.

The B_1 horizon, a heavy silt loam, occasionally with varying amounts of sand, varied in color from dull brown to yellowish brown. Encountered at 9 inches, it was 4 inches thick. The soil had a well-marked, small blocky structure which was more evident than in the A_2.

The B_2 horizon, encountered at 13 inches, was 19 inches thick and consisted of a heavy, reddish brown sandy clay. It had a characteristic angular nut structure which became more massive as the C horizon was approached. At the upper limits of the C_1, the nut structure disappeared. Upon wetting, the B_2 horizon becomes very sticky and plastic. Upon drying, the individual blocks shrink and the sutures give rise to marked hair-line crevices. Isolated white to light yellow particles of cherty material of variable size characterized the horizon, particularly in the lower portions.

Appearing at a depth of 32 inches, the C horizon consisted of a gravelly sandy clay or a gravelly sandy loam. Limestone rocks were found in variable numbers and sizes in the upper 6-inch level of the horizon.

This soil type is subject to erosion, evidenced by exposure of the A_2 and, occasionally, B_1 horizons in scattered areas. Erosion is not confined to areas with marked slopes but also occurs on comparatively level surfaces.

Vegetation

Deciduous forest is the climatic climax in the region. In the southeastern portion of Walworth County it was originally represented by a mixture of several species of oak, maple, hickory, etc. (17). At present the forest at Wychwood, one of the few relatively undisturbed stands in the region, is primarily sugar maple–red oak–white oak. The older oaks are more than 200 years old, while many maples are 100 years or more.

TABLE 1

RELATIVE ABUNDANCE* AND FREQUENCY INDEX OF STATION SPECIES

SPECIES	STATION†																FREQUENCY INDEX (%)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
A. Herbaceous:																	
Actea alba	...	...	...	...	...	R	...	...	...	...	...	...	R	...	...	R	19
Adiantum pedatum	...	...	R	...	...	...	...	...	...	...	...	...	...	...	...	...	6
Amphicarpa bracteata (p)‡	...	...	...	...	R	...	...	C	C	...	R	A	...	R	...	...	38
Aralia nudicaulis (p)	...	...	...	C	R	...	...	R	...	...	C	C	R	C	C	R	56
Arisaema triphyllum (p)	R	C	C	...	...	C	R	C	C	C	...	C	...	R	R	...	69
Aster sp.	...	...	...	...	...	C	...	R	R	...	R	C	R	...	C	C	50
Carex pennsylvanica (p)	...	...	...	A	A	R	...	...	...	...	A	C	R	R	C	...	50
Caulophyllum thalictroides (p)	R	R	...	R	...	...	R	C	C	R	...	...	...	...	C	...	50
Circaea latifolia	...	...	...	...	...	C	...	...	...	...	...	...	...	...	C	...	13
Cryptotaenia canadensis	...	...	...	...	...	C	...	...	...	...	...	...	...	...	...	...	6
Cypripedium parviflorum	...	...	...	...	...	...	...	...	...	...	R	...	...	...	...	...	6
Desmodium strictum (p)	...	...	...	R	...	...	...	...	...	...	R	R	R	...	C	R	38
Dioscorea villosa	R	...	...	...	...	...	...	C	R	...	R	C	R	...	...	...	38
Eupatorium purpureum (p)	...	...	...	...	...	C	...	...	R	R	...	...	...	...	R	R	31
Eupatorium rugosum (p)	...	...	R	R	...	...	...	C	R	...	...	...	...	...	R	C	38
Galium sp.	...	...	...	...	...	...	...	...	...	...	...	...	R	R	R	R	25
Geranium maculatum (p)	...	...	R	R	R	C	R	C	R	...	R	C	...	...	C	C	69
Geum sp.	...	...	...	...	...	...	R	...	...	...	...	...	...	...	...	...	6
Hepatica acutiloba (p)	...	...	...	...	...	C	...	R	C	...	R	R	R	R	...	...	44
Helianthus sp.	...	...	...	...	R	...	...	...	...	...	R	...	...	...	...	...	13
Laportea canadensis (p)	...	...	...	...	...	R	...	...	...	...	...	...	...	...	...	...	6
Menispermum canadense (p)	...	...	...	...	...	C	...	...	...	...	...	...	...	...	...	...	6
Osmorhiza claytoni	...	...	...	R	...	...	...	...	...	...	...	...	...	...	...	...	6
Phryma leptostachya (p)	...	...	...	...	...	C	...	...	...	...	...	...	...	...	...	...	6
Podophyllum peltatum (p)	R	R	R	...	...	C	R	R	R	R	C	C	R	...	...	C	75
Polygonatum pubescens (p)	...	...	R	R	R	...	...	C	C	...	...	...	...	R	C	...	44
Prenanthes sp.	R	...	...	R	...	...	...	...	...	...	...	R	...	...	...	...	19
Ranunculus septentrionalis (p)	...	...	...	...	...	...	...	...	R	...	R	...	...	R	...	...	19
Sanguinaria canadensis	...	...	R	...	...	...	...	C	...	...	...	...	...	R	...	...	19
Sanicula sp.	...	...	...	...	...	R	...	...	...	...	...	...	...	...	...	...	6
Smilacina racemosa (p)	...	C	C	...	C	...	R	C	C	C	C	R	R	R	C	C	81
Smilax ecirrhata (p)	R	R	R	...	...	...	...	R	R	...	R	...	...	...	C	...	44
Solanum dulcamara (p)	...	...	...	...	...	R	...	...	...	...	...	...	...	...	...	...	6
Solidago latifolia (p)	R	R	C	C	R	...	C	C	C	C	C	C	C	R	C	C	94
Solidago sp.	...	...	...	R	R	...	...	...	...	R	R	C	R	R	C	...	50
Thalictrum dioicum (p)	...	...	...	...	...	...	...	...	...	R	R	...	...	...	C	...	19
Trillium grandiflorum	...	...	...	...	...	R	...	R	...	...	...	...	R	...	...	...	19
Trillium recurvatum	...	...	...	...	...	...	...	...	R	...	...	...	...	...	...	...	6
Uvularia grandiflora (p)	...	...	...	...	...	C	R	C	C	C	R	...	...	R	C	...	50
Viola sp.	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	C	6
No. of species per station	7	6	10	11	9	17	8	17	17	9	18	14	13	13	18	12	.....

* Relative abundance: A, abundant; C, common; R, rare.

† Stations 1–10 sampled in 1938; stations 11–16 sampled in 1939.

‡ (p), one or several plants or their root systems photographed in 1938–1940.

TABLE 1—*Continued*

Species	Station†																Frequency index (%)
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
B. Woody:																	
Acer saccharum (p)	A	A	A	C	C	C	A	C	A	A	A	A	A	A	A	A	100
Amelanchier canadensis	...	...	...	...	...	...	...	C	...	...	R	...	C	C	...	...	25
Carya cordiformis	...	...	R	...	C	C	C	...	C	...	...	...	R	R	C	R	56
Cornus alternifolia	...	...	C	...	...	...	...	...	...	...	...	R	...	...	R	...	19
Fraxinus americana (p)	C	...	C	C	C	C	...	R	C	C	C	C	C	A	A	C	88
Fraxinus nigra	...	...	...	...	...	...	...	R	...	...	R	...	...	...	...	...	13
Hamamelis virginiana	...	...	R	...	...	...	...	...	...	...	...	C	...	...	...	...	13
Lonicera dioica (p)	C	...	...	C	...	...	...	...	...	...	C	C	A	R	R	...	44
Ostrya virginiana	...	C	R	C	C	...	...	C	C	C	C	C	C	...	C	C	75
Parthenocissus quinquefolia (p)	...	...	C	R	R	C	A	C	C	R	C	R	R	...	A	...	75
Prunus serotina	R	...	R	R	...	...	...	...	...	...	R	...	...	C	...	...	31
Prunus virginiana (p)	C	C	C	C	...	...	C	...	C	C	...	R	C	C	R	C	75
Quercus alga (p)	...	C	R	C	C	C	C	C	R	...	A	A	C	C	C	C	88
Quercus borealis maxima (p)	C	A	C	A	A	C	C	A	C	R	C	C	A	A	A	C	100
Rhus radicans	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	C	6
Ribes cynosbati	...	...	...	...	...	...	...	...	...	...	...	...	C	R	...	...	13
Tilia americana	C	C	...	...	...	...	C	...	C	C	C	...	A	C	C	C	63
Ulmus americana (p)	...	R	...	...	...	...	...	...	R	...	...	C	...	...	R	...	25
Ulmus fulva	C	...	R	...	...	...	...	...	...	...	...	C	C	C	C	C	44
Viburnum acerifolium	...	...	...	C	A	...	...	...	...	C	C	C	C	...	R	R	50
Vitis sp.	...	...	...	...	...	...	...	...	...	...	R	...	...	...	...	C	13
Zanthoxylum americanum	C	R	...	...	...	...	C	...	...	...	R	...	R	...	...	...	31
No. of species per station	9	8	12	10	8	6	8	8	10	8	14	13	15	12	14	12	.....

A detailed cover or frequency analysis of the vegetation was not made.[1] Table 1 shows the presence, relative abundance, and frequency index of species found, based on circular areas 25 yards in diameter around each trench.

The stations were designated numerically, since they could not be differentiated individually by any one characteristic. While it would be desirable to classify the sixteen stations on the basis of vegetation, it was impractical and confusing since their floristic composition was not sufficiently variable and other factors in the selection of a station were slighted unwarrantedly.

Investigation

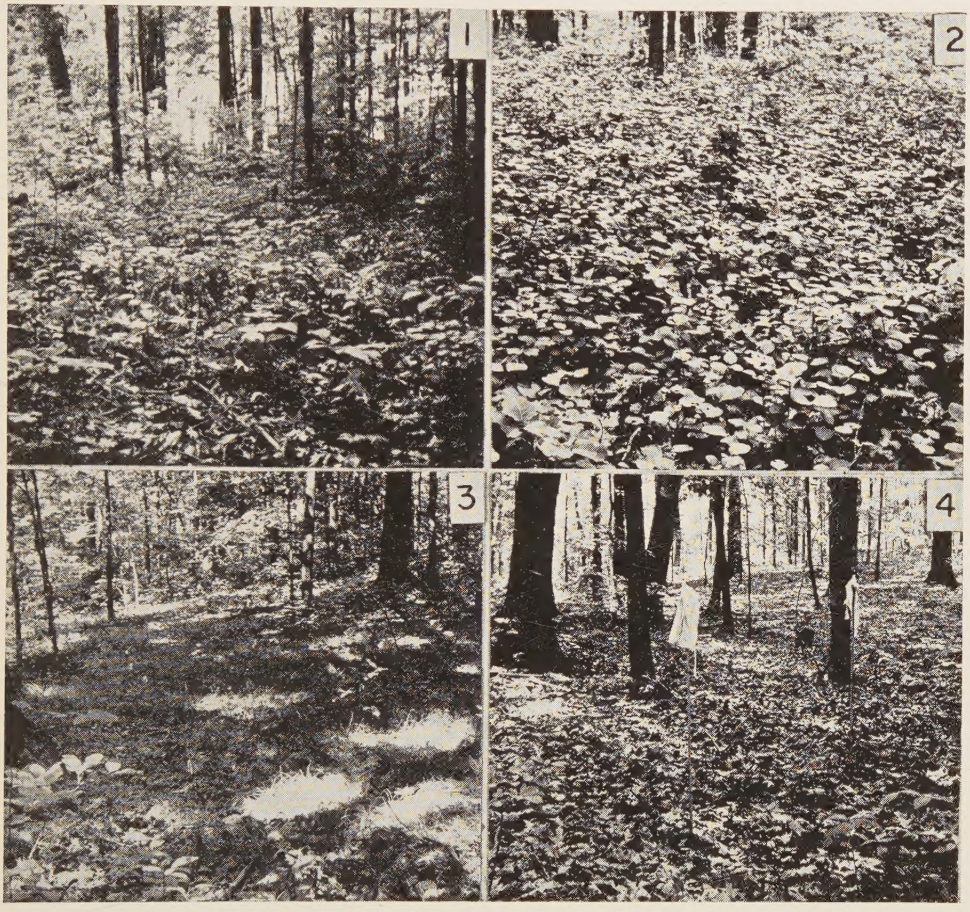
General methods

The sixteen stations were selected on the basis of relative abundance and type of herbaceous and woody ground cover, nature of soil, and topographical situation. A cross-sectional sample of conditions within the forest was thus obtained.

[1] Dr. Charles E. Olmsted, under whom this study was completed, has been conducting an investigation of the environment of this forest for a period of 6 years. The data, when published, will provide a treatment of the floristic composition.

Those station types which occupied the larger areas were sampled several times to assure reasonably accurate measurement of their root distribution and development (figs. 1–4).

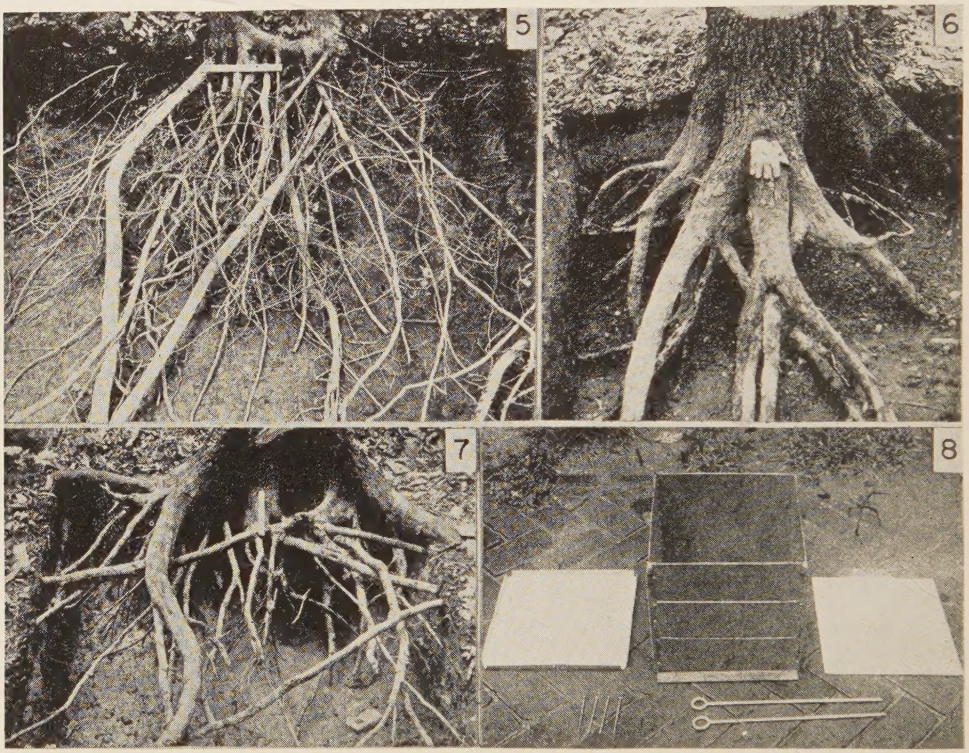
The methods used at stations 1–10 were, with some variations, similar to those initially employed by WEAVER (18) and those recently followed by TURNER (16),



FIGS. 1–4.—General views of some station types. Fig. 1, station 9; fig. 2, station 13; fig. 3, station 4; fig. 4, station 2.

BILLINGS (2), LUTZ, ELY, and LITTLE (10), and COILE (3). The rectangular trenches employed were $7\frac{1}{2} \times 2\frac{1}{2}$ feet. The area charted was 6 feet long horizontally, to the depth of the trench vertically, and on the wall nearest magnetic north. Stations 11–16 were sampled by a new method in which equal areas of all four walls of a square trench were charted. Such trenches were 4 feet square. The area charted on each wall was 3 feet long and to the depth of the trench (fig. 21).

After a station was chosen, either a rectangular or square trench was opened in a representative area sufficiently removed from trunks of any large trees and to a depth in the C horizon averaging 3–3½ feet, where the roots were significantly few in number. Vertical walls were maintained and roots projecting into the trench were cut off. After the wall or walls to be charted had been cleaned, the horizontal

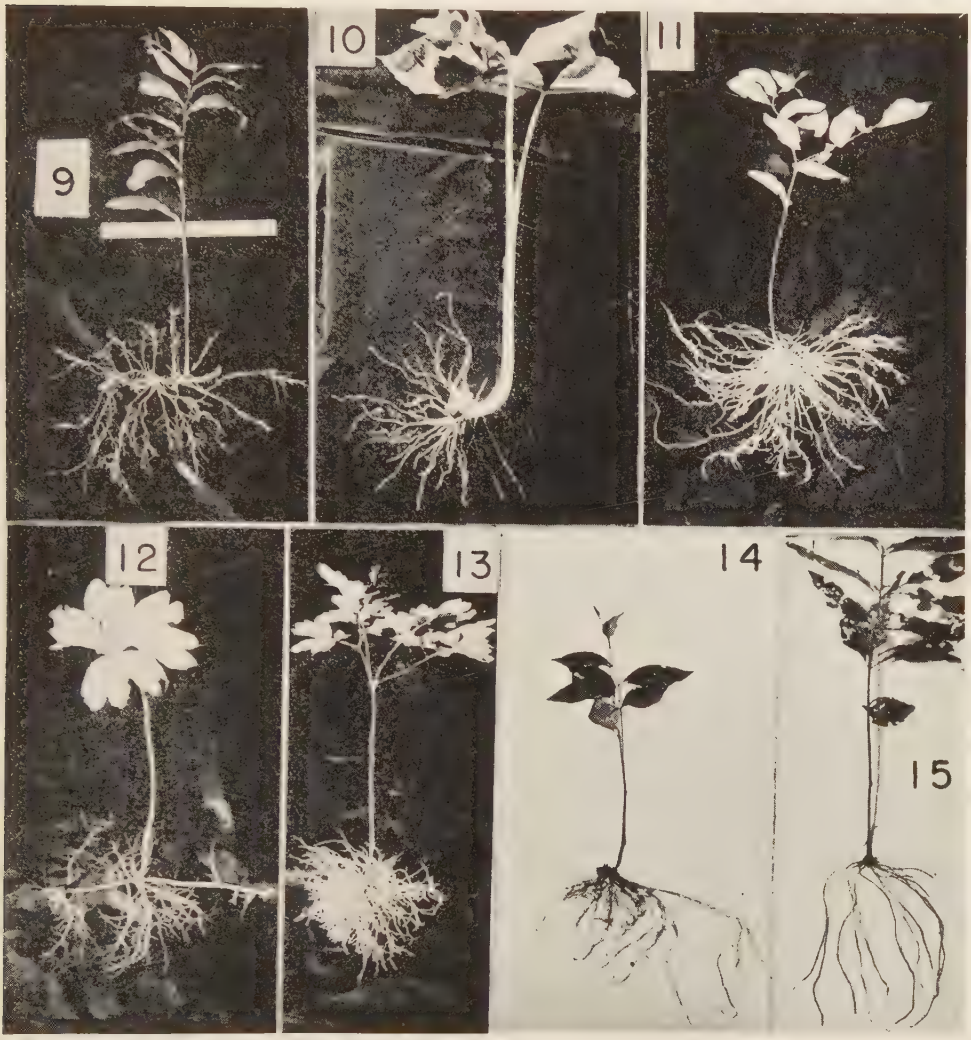


FIGS. 5–8.—Figs. 5–7, excavated specimens of dominant tree species: 5, *Acer saccharum;* 6, *Quercus alba;* 7, *Quercus borealis maxima.* Fig. 8, soil sample box for root-volume determinations.

boundaries of the profile were marked. Each area was ruled into square feet by horizontal and vertical strings. The horizons were charted on a scale of 3 inches to 1 foot.

A heavy, square-foot wire frame, divided into 2-inch squares by fine wire, was used in charting all profile inclusions. This was placed successively on each square foot of the trench face, which was carefully worked over with a fine pointed instrument to locate all root ends. Living, dead, woody, and herbaceous roots were then charted. Seven diameter size classes were recognized: 0–1, 1–2, 2–3, 3–4, 4–5, 5–10, and > 10 mm.

After charting the roots, the horizons were examined for other characteristics and possible inclusions. Counts were made of earthworms and cicada nymphs,

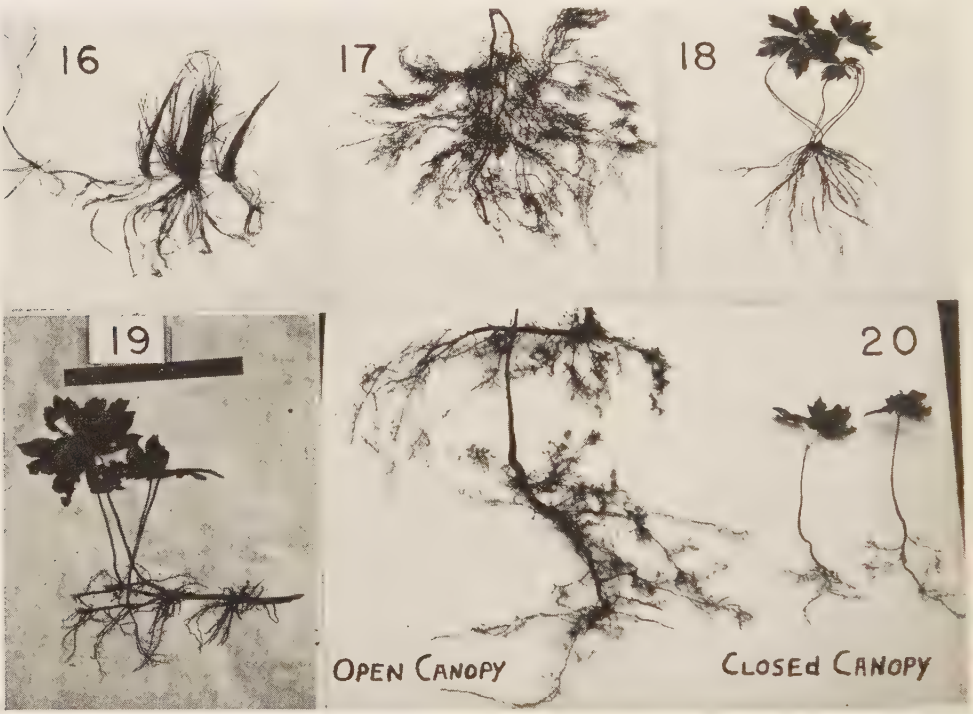


FIGS. 9–15.—Root systems of some native species. Fig. 9, *Smilacina racemosa;* fig. 10, *Arisaema triphyllum;* fig. 11, *Uvularia grandiflora;* fig. 12, *Podophyllum peltatum;* fig. 13, *Caulophyllum thalictroides;* fig. 14, *Phryma leptostachya;* fig. 15, *Eupatorium purpureum.*

and their burrows were recorded on the profile chart. The root systems of characteristic woody seedlings and herbaceous species, located either at or near the edge of a trench, were excavated and their relations to the surface horizons

noted. In other cases the soil was washed away from excavated blocks. The entire plants, or occasionally only their root systems, were photographed (figs. 9–20).

Root volumes were determined in the upper cubic foot of soil in different station types. For this purpose a soil-sample box was devised, permitting the subdivision



FIGS. 16–20.—Root systems of some native species. Fig. 16, *Carex* sp.; fig. 17, *Solanum dulcamara;* fig. 18, *Geranium maculatum;* fig. 19, *Parthenocissus quinquefolia;* fig. 20, *Acer saccharum* (1036 seedlings from open and closed canopies).

of a sample into three successive sections, each 4 inches in depth. The box was constructed of $\frac{1}{16}$-inch rolled-sheet steel welded to give an inside volume of 1 cubic foot. The bottom edges were beveled to make a sharp cutting edge. The plate used to divide the total sample into three units, 4 inches deep, was driven, guided by two slightly raised lips, through two narrow slots on one side of the box. By successive driving and digging around the box, an accurate cubic-foot sample, with its roots, could be obtained (fig. 8). Roots $1\frac{1}{2}$–2 inches in diameter were easily cut in preliminary sampling. Root volumes were measured by displacement in water.

Statistical methods

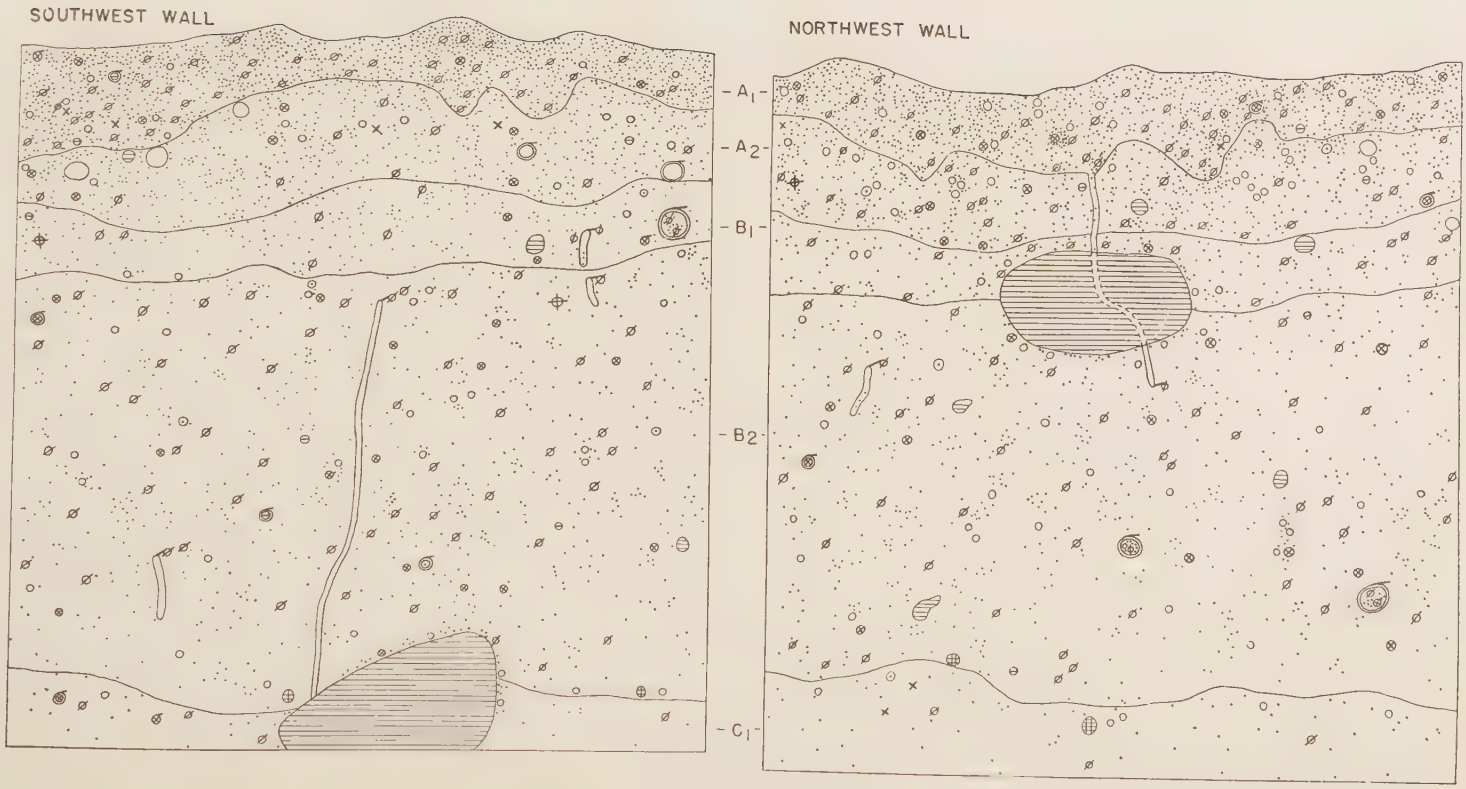
In measuring the degree of heterogeneity exhibited by the root distribution in the various station types, it was necessary to treat the data statistically. The standard deviation of means, that is, standard error (standard error $\sqrt{\frac{\Sigma V^2 - \frac{(\Sigma V)^2}{N}}{N(N-1)}}$, where Σ is the symbol for summation, V is the individual observation, and N is the number of variants) was obtained for each wall of square trenches as well as for total root data of the four walls.[2] Accordingly, the limits within which variations of the means occur because of uncontrollable conditions were defined. The standard error of the difference (standard error of difference $= (S.E._x)^2 - (S.E._y)^2$, where $S.E._x$ and $S.E._y$ are the standard errors of the means of x and y, respectively, was determined when two walls of the same square trench were compared. The t test for significance was used accordingly ($t = \frac{\bar{D}}{S.E._{\bar{D}}}$, where $\bar{D}$ is the difference between means and $S.E._{\bar{D}}$ is the standard error of the difference). The value t was used to determine the probability (P) according to the table for P values as given by Fisher (5). Differences not significant at the 0.05 level were not considered statistically significant (14).

Soil factors

The soil surface about station types with sparse ground cover (stations 1, 2, 3, 14, and 16) showed varying degrees of erosion, evidenced by the partial exposure of tree roots 2 -3 inches in diameter and the occasional appearance of the A_2 and B_1 horizons. Judged by its typical grayish yellow color, the A_2 horizon was absent in portions of the profile sections in stations 7 and 9. In stations 4, 5, and 11, with ground cover predominately of sedge, all horizons were characterized by greater sandiness than at other stations.

In all profiles, the B_2 horizons (of heavy, reddish brown sandy clay) possessed the greatest depth and compactness. It typically showed many roots penetrating along the sutures formed by the irregular nut structure. The smallest roots (0.1–1.0 mm.) frequently were found penetrating the smaller soil blocks in the upper portions of the horizon, while this condition was relatively rare in the lower, more compact soil with larger blocks. Resistance to root penetration was evident from the flattened form of the smaller roots (< 2 mm.), when following the suture lines. Internal drainage is greatest along the sutures of the nut structure. It appeared comparatively favorable except in stations 1, 2, 3, 14, and 16, where greater

[2] Square trenches readily permit application of statistical methods. Accordingly, statistical treatment was confined to comparisons of variability in root numbers among station types sampled by such trenches and among their four walls (table 7).


SOUTHWEST WALL
NORTHWEST WALL
A1
A2
B1
B2
C1

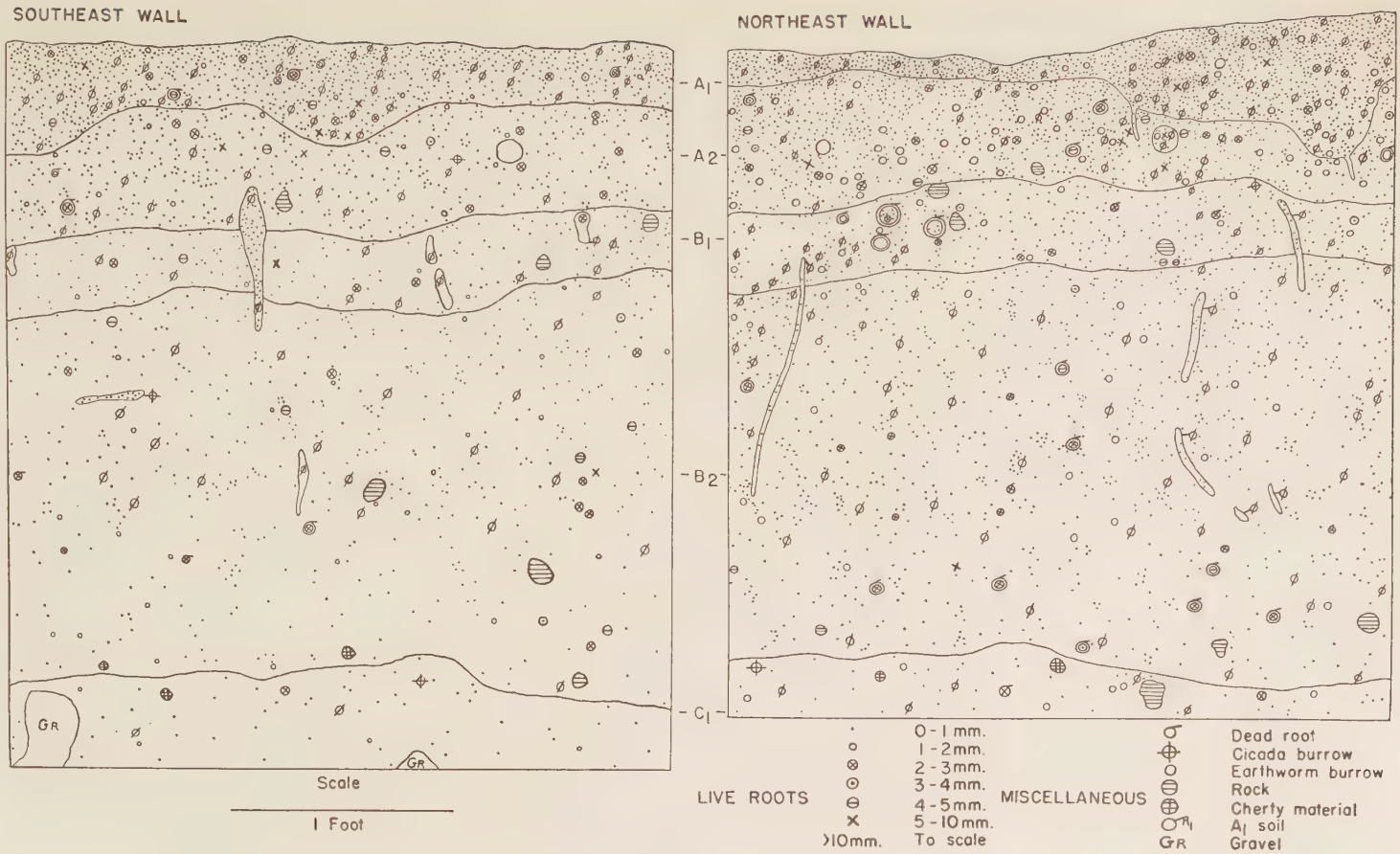


FIG. 21.—Root distribution and other horizonal inclusions in S.W., N.W., S.E., and N.E. profile walls of station 12; 1939

plasticity of the B_2, with marked increase in the clay content, interferes with percolation. Conversely, conditions for greatest drainage were found in stations 4, 5, and 11, with distinctly sandier profiles.

The surface soil of all stations exhibited numerous earthworm (*Lumbricus* spp.) middens (6) of variable diameter and height. Typically they were 4–5 inches wide and 1–1½ inches high. Cross-sections of some of the middens and accompanying burrows have shown leaf blades and petioles, in various stages of decomposition, to a depth of 6–8 inches. Burrows of smaller earthworms were also found. The larger burrows were lined with a film of dark organic soil which originated from worm castings; the burrows of the smaller earthworms had no visible organic soil lining. Apparently lining of burrows is accomplished over several years of active use. Middens play an important part in giving the surface soil an irregular local topography. Their black, highly organic soil withstands erosion very effectively. Some of the height of those located on slopes was developed by erosion about them.

Earthworms are the most conspicuous group of animals appearing in the profile sections. Greatest activity was manifest in the A_1 horizon, where they are largely responsible for the soil's porous nature. Numerous castings studded the middens proper and the soil surface at some distance from them. Burrows were found also throughout midden-less areas. The worms apparently play as important a role in mixing and aerating the surface horizons (A_1 and A_2) as they do in breaking down the leaf litter. In the latter case it is known that earthworms do eat leaf materials (4), yet their over-all effect upon breakdown of leaf litter probably centers about creation of a more favorable environment for bacteria and fungi through movement of leaves into the burrows.

In all profiles, regardless of the resistant nature of the B horizons, earthworms and their burrows were found in the C horizon at depths of 3–3½ feet, and in deeper trenches at 5 feet. The burrows were fairly perpendicular, with deviations largely where rocks blocked the path. No differences in depth of penetration were found in the profiles investigated.

The periodical cicada, *Magicicada septendecim* (15), was also conspicuous. The stage initially encountered in 1938 was the fifth instar or last stage prior to the adult. The former emerged during the spring of 1939. The varied nymph and pupal stages (1, 12) of the insect had penetrated the profile to depths of 3–3½ feet. In 1938 some nymphs were found in pockets which, approximating ½-inch in diameter and ¾–1 inch in height, just housed them. More typically this chamber extended upward several inches, a nymph lying at the bottom. In the latter cases the nymphs apparently had started their upward movement through the soil, but such burrows ended abruptly in either the B_2 or C_1 horizon. They were never found in the upper horizons (A_1, A_2, or B_1).

Burrows, formed by nymphs in the previous generation, had apparently been filled.[3] The trenches opened in 1939 revealed the burrows resulting from emergence of the nymphs. Mounds, built by the nymphs over the mouths of their burrows, were composed of B horizon soil, had an average basal diameter of 1 inch and a height of $1\frac{1}{2}$–$2\frac{1}{2}$ inches, with walls $\frac{3}{16}$–$\frac{4}{16}$ inch thick. They typically were confined to wooded areas where organic forest debris was abundant on the surface soil. In open areas outside the forest such mounds were rare.

Open cicada burrows, extending almost perpendicularly from their surface openings to varying depths, were common in all profiles investigated in 1939 and 1940. On 30-meter quadrats sampled at random, an average of fourteen cicada mounds per square meter was found.

In the A_2, B_1, and B_2 horizons of all profiles occurred varying-sized pockets of A_1 soil, from the filling-in of old root holes after root decay. Similar smaller pockets were apparently the result of earthworm activity, particularly in the A_2. The castings were conclusive evidence in differentiating these latter pockets from filled-in root holes, which also often contained fragmentary and undecomposed portions of roots. Some A_1 soil probably washes into earthworm burrows. Small herbaceous and woody roots often were found where, as a result of the union of several adjacent burrows, pockets of dark soil were developed with diameters of $\frac{1}{2}$ inch or more. This was also true in root holes which had been filled to the lower levels of the B_2 horizon. The concentration of roots in such pockets frequently approached, and occasionally equaled, that typical of the A_1 horizon. The roots in such pockets did not have the flattened form typical in the B_2. Some pockets of apparently A_1 soil in the B horizons, approximating $\frac{1}{2}$ inch in diameter, were probably the filled-in burrows of the cicada nymphs which emerged in 1922. Still larger pockets (6–8 inches in diameter) probably were filled-in burrows of rodents.

Root data

The basic data on root distribution (table 2) indicate the total number of live roots in the horizons of each station. The seven size classes recognized are differentiated into two groups, < 1 mm. and > 1 mm. The number of roots per square foot of horizon surface was greatest in horizons A and B, the former always with a much larger number than the latter. The number of roots per square foot of C horizon was low in all cases. The apparent relative suitability of horizons A_1, A_2, B_1, B_2, and C_1 for root development, as measured by numbers, decreased—with a few exceptions—in passing downward. With the exception of stations 5, 7, and 15, the greatest total decrease in root numbers per square foot of horizon surface occurred in passing from the A_1 to the A_2, although the latter was encountered

[3] Mr. William P. Longland, superintendent of Wychwood, stated that cicada nymphs had emerged in exceedingly large numbers in 1922. He judged the numbers in 1939 to be equally as great.

at the relatively slight average depth of 4 inches. These three stations showed marked exception to the typical root distribution.

TABLE 2

NUMBER OF LIVE ROOTS PER PROFILE HORIZON

Horizon	Total no. of roots	No. of roots per square foot of rock-free area		Total no. of roots	No. of roots per square foot of rock-free area		Total no. of roots	No. of roots per square foot of rock-free area		Total no. of roots	No. of roots per square foot of rock-free area	
		<1 mm.	>1 mm.		<1 mm.	>1 mm.		<1 mm.	>1 mm.		<1 mm.	>1 mm.
	Station 1*			Station 2			Station 3			Station 4		
A_1	460	116	31	591	450	23	1067	423	55	2072	1028	41
A_2	230	33	14	273	87	20	311	166	22	684	218	25
B_1	50	12	3	111	46	11	523	91	15	453	89	9
B_2	99	8	2	380	27	4	137	46	5	364	69	6
C_1	14	5	.....	13	7	2	166	33	1	403	55	6
	Station 5			Station 6			Station 7			Station 8		
A_1	1857	1289	6	2487	657	30	1185	526	16	1781	870	21
A_2	1495	740	71	436	222	11	451	649	29	797	213	11
B_1	315	130	14	383	138	8	785	461	23	375	172	13
B_2	965	68	6	644	116	7	1537	157	9	772	66	6
C_1	11	9	2	270	70	1	18	68	.....	65	32	3
	Station 9			Station 10			Station 11			Station 12		
A_1	1912	680	31	1873	868	22	3541	891	31	3897	1094	24
A_2	256	381	29	1060	353	21	2268	371	22	2510	464	28
B_1	405	195	11	379	225	18	862	216	10	927	252	12
B_2	1070	98	7	1074	93	7	3021	133	8	3009	136	8
C_1	180	107	8	181	91	3	431	57	4	220	65	7
	Station 13			Station 14			Station 15			Station 16		
A_1	4656	820	50	2043	554	28	1595	354	41	1666	453	57
A_2	1763	321	26	1281	207	15	1081	378	53	1004	129	18
B_1	721	211	11	438	177	11	362	161	17	416	114	16
B_2	1707	113	10	1695	87	9	1443	59	7	852	55	13
C_1	456	42	5	410	49	4	206	37	4	314	22	7

* Data for stations 1–10 based on one wall 6 feet long; for stations 11–16, on four walls totaling 12 feet long.

A concentration of the smallest roots, 0.1–1.0 mm. in diameter, was found in the A_1 horizon (table 2), indicating the location of much of the root water-absorbing

surface. This size class, per unit area, decreased markedly in the lower horizons. Contrary to possible expectations, the larger roots (> 1 mm.) showed no increase in numbers per unit horizon surface below the A. Further, within the A horizon only stations 5, 7, and 15 showed such an increase in the A_2 as compared with the

TABLE 3

ROOT NUMBERS AND PERCENTAGE ROOT AREA PER SQUARE FOOT OF ROCK-FREE HORIZON SURFACE*

Station	Root unit	Horizon				
		A_1	A_2	B_1	B_2	C_1
1	No.	147	47	15	10	5
	Area	1.913	0.341	0.025	0.029	0.001
2	No.	473	107	57	31	9
	Area	0.535	0.365	0.399	0.122	0.052
3	No.	478	188	106	51	34
	Area	1.291	0.217	0.119	0.012	0.004
4	No.	1069	243	98	75	61
	Area	0.676	0.276	0.162	0.025	0.096
5	No.	1295	811	144	74	11
	Area	0.441	1.459	0.243	0.031	0.006
6	No.	687	233	146	123	71
	Area	1.817	0.157	0.321	0.248	0.017
7	No.	542	678	484	166	68
	Area	0.275	0.407	0.584	1.023	0.001
8	No.	891	224	185	72	35
	Area	0.360	0.204	1.363	0.581	0.015
9	No.	711	410	205	105	115
	Area	0.813	0.138	1.360	0.447	0.108
10	No.	890	374	243	100	94
	Area	0.987	0.423	0.217	2.115	0.031
11	No.	922	293	226	141	61
	Area	0.723	0.555	0.195	0.121	0.064
12	No.	1118	492	264	144	72
	Area	0.758	1.078	0.301	0.099	0.075
13	No.	870	347	222	123	47
	Area	2.116	0.642	0.180	0.176	0.111
14	No.	582	272	188	96	53
	Area	0.948	0.391	0.218	0.093	0.064
15	No.	395	431	178	66	41
	Area	0.416	1.459	0.309	0.093	0.025
16	No.	510	147	130	68	29
	Area	0.647	0.221	0.259	0.240	0.257

* Here and in subsequent tables, profile data for stations 1–10 based on one wall 6 feet long; for stations 11–16, on four walls totaling 12 feet long.

A_1. Greatest numbers of dead roots were found in the lower horizons. The smaller roots (< 5 mm.) were found dead more frequently.

From the root distribution recorded on the charts in the field, the number of living roots and the percentage cross-sectional area occupied by them were calculated on three different bases for each station. These were (*a*) root numbers and percentage area per square foot of rock-free horizon surface (table 3); (*b*) root

numbers and percentage area per square foot of rock-free vertical profile sections occupying 0–1, 1–2, 2–3 foot depths (table 4); and (*c*) root numbers and percentage area per square foot of vertical profile sections 3 feet in depth (table 4). Root areas were obtained by use of the seven diameter size classes. Roots 0.1 –1.0

TABLE 4

ROOT NUMBERS AND PERCENTAGE ROOT AREA PER SQUARE FOOT OF ROCK-FREE VERTICAL PROFILE SECTIONS 0–1, 1–2, 2–3, AND 0–3 FEET DEEP

Station	Depth (feet)	Root no.	Root area (%)	Station	Depth (feet)	Root no.	Root area (%)
1	0–1	96	1.191	9	0–1	444	0.361
	1–2	15	0.047		1–2	105	0.059
	2–3	10	0.029		2–3	79	0.035
	0–3	41	0.422		0–3	209	0.152
2	0–1	163	0.438	10	0–1	525	0.255
	1–2	41	0.139		1–2	130	0.199
	2–3	23	0.065		2–3	123	0.178
	0–3	76	0.214		0–3	259	0.211
3	0–1	275	0.606	11	0–1	528	0.547
	1–2	60	0.030		1–2	179	0.157
	2–3	25	0.003		2–3	96	0.114
	0–3	120	0.214		0–3	268	0.273
4	0–1	477	0.386	12	0–1	603	0.767
	1–2	88	0.097		1–2	174	0.167
	2–3	82	0.094		2–3	95	0.084
	0–3	216	0.192		0–3	291	0.339
5	0–1	607	0.865	13	0–1	573	1.249
	1–2	99	0.032		1–2	137	0.113
	2–3	48	0.028		2–3	65	0.101
	0–3	251	0.308		0–3	258	0.488
6	0–1	501	0.359	14	0–1	330	0.501
	1–2	135	0.067		1–2	98	0.238
	2–3	84	0.005		2–3	55	0.112
	0–3	240	0.143		0–3	161	0.284
7	0–1	486	0.305	15	0–1	284	0.572
	1–2	143	0.064		1–2	62	0.081
	2–3	55	0.012		2–3	40	0.041
	0–3	228	0.127		0–3	129	0.231
8	0–1	467	0.213	16	0–1	233	0.307
	1–2	113	0.208		1–2	76	0.213
	2–3	48	0.024		2–3	34	0.342
	0–3	210	0.148		0–3	114	0.287

mm. were assigned diameters of 0.75 mm. Exact diameters of roots > 10 mm. were obtained in the field. Accepted diameters of the five remaining size classes were the midpoints of their ranges.

Based on root numbers and percentage root area per square foot, the suitability for root growth of the specific horizons A_1, A_2, B_1, B_2, and C_1 was variable. Twelve stations showed both greater root numbers and higher percentage root area in the A_1 than in the A_2. Of the other stations, only two—stations 7 and 15—showed both greater root numbers and area in the A_2 than in the A_1. The latter stations were

selected because a dense and homogeneous layer of *Parthenocissus quinquefolia* dominated the ground cover of both areas. The roots of this species are found almost exclusively in the upper portions of the A_2 horizon. In station 5 there was a higher percentage of root area in the A_2 horizon but not a greater number of roots. Here the difference coincided with the association of a large number of small shrubs with comparatively homogeneous patches of sedge. In no station did the B_1 horizon show both greater root numbers and percentage root area than did the A_2. This was true successively in the B_2 and C_1, where the influence of large roots upon the calculated area gave higher values that were not significant. In terms of both root area and numbers, however, the B_2 and C_1 horizons exhibited the least suitability for root development and showed less variation from the one to the other than did the upper horizons. These general statements, with the few exceptions, hold true regardless of the peculiarities of the different stations.

The greater total and percentage decreases of both root number and area, in profile sections 0·1, 1–2, and 2·3 feet in depth (table 4), occurred in passing into the second foot. The decrease was less from the second to the third foot. Station 8 decreased more in area in passing from the second to the third foot but showed typical decreases in root numbers with increased depth. The greatest root area in station 16 occurred in the third-foot section. These two stations, however, showed greater total and percentage decrease of root numbers from the first to the second foot level. Generally, the larger the root numbers and total area in the top sections, the greater the percentage decrease at the second foot level. Root frequency definitely decreases with increased depth.

Profile areas 3 feet in depth (table 4) at stations 1, 2, 3, 14, and 16, selected because of dearth of ground cover, were characterized by comparatively large percentage root areas and small root numbers, that is, few but large roots. Stations 4–13 and 15, with abundant ground cover of varied floristic composition, were characterized by large root numbers and small average root areas (table 2). Station 15, an exception to this general condition, had an average area per root approximately equal to that of station 14, which possessed the smallest average area per root of the five "bare" stations. This can be explained in part by the association of a number of woody species (table 1) with the society of *Parthenocissus* sampled at the former station, influencing the number of roots > 1 mm.

The number of earthworm burrows per square foot of profile areas indicated great activity in all station types. Such burrows occurred less frequently in stations where patches of sedge were associated with sandier silt loam soils. The greatest number of cicada pupae and burrows were found where red oaks were dominant in the canopy, but the nymphs and their burrows were found in all the trenches (table 6). Such burrows afforded significant drainage during rains heavy enough to yield run-off.

The total volume of roots in an upper cubic foot of soil was variable throughout the station types (table 5). Areas with sparse ground cover yielded root volumes equal to those of areas with abundant ground cover. In samples which contained no roots $> \frac{1}{2}$ inch in diameter, root volume decreased successively in the 0–4, 4–8,

TABLE 5

VOLUME OF ROOTS IN ONE CUBIC-FOOT SOIL BLOCKS SUBDIVIDED INTO 4×12×12 INCH SECTIONS

Sample	Ground cover type	Depth of soil block section (inches)	Percentage root volume	
			Per soil block section (4×12×12 inch)	In total cubic foot
1	Mixed mesic spp.	0–4	0.481	0.261
		4–8	0.167	
		8–12	0.136	
2	Mixed mesic spp.	0–4	0.659	0.453
		4–8	0.628	
		8–12	0.073	
3	Bare	0–4	0.963	2.164
		4–8	4.272	
		8–12	1.256	
4	Bare	0–4	0.235	0.535
		4–8	1.361	
		8–12	0.010	
5	C. pennsylvanica society	0–4	1.717	1.148
		4–8	1.549	
		8–12	0.178	
6	C. pennsylvanica society	0–4	2.795	2.494
		4–8	4.550	
		8–12	0.136	
7	Lonicera dioica society	0–4	1.413	0.530
		4–8	0.157	
		8–12	0.020	
8	Lonicera dioica society	0–4	1.895	0.813
		4–8	0.471	
		8–12	0.073	
9	Parthenocissus sp. society	0–4	0.701	0.656
		4–8	1.151	
		8–12	0.115	
10	Parthenocissus sp. society	0–4	1.266	0.484
		4–8	0.104	
		8–12	0.083	

and 8–12 inch levels. When the sample contained larger roots, the volume frequently was largest in the 4–8 inch level; but the 8–12 inch section never surpassed the 4–8 inch level. In all samples the 0–8 inch section contained 80 per cent or more of the total root volume.

The root systems of typical herbaceous and woody seedlings predominately

were confined to the upper 6 inches of the profile (figs. 9–20). Exceptions occurred in areas where openings in the canopy have existed for several years. There most root systems extended to depths of 12–18 inches.

The root systems of the selected specimens of the three dominant species of the forest—sugar maple, red oak, and white oak—were investigated in 1940 (figs. 5–7). The white oak, 223 years old, 23 inches in diameter at a height of 2 feet, was wind-

TABLE 6

COMPARATIVE STATION TYPE DATA

Station	Physiography		Depth to C_1 horizon (inches)	Important species of ground vegetation	No. of species with 50–100% frequency index		Earthworm burrows per square foot	Cicada burrows per total profile
	Character of topography	Elevation (feet)			Herbaceous (11 species recorded)	Woody (10 species recorded)		
1...	Southeast slope, 2.5°	961	36–42	Mesic woodland herbs and shrubs (rare)	4	5	14	3
5...	South slope, 4.5°	1019	36–43	Carex pennsylvanica (abundant)	6	8	8	3
7...	Southeast slope, 7.5°	1017	32–38	Parthenocissus quinquefolia (abundant)	7	7	7	6
8...	South slope, 4.5°	909	36–40	Mesic woodland herbs and shrubs (abundant)	9	6	9	3
11...	North slope, 3.5°	1011	29–36	C. pennsylvanica (abundant)	9	8	9	15
12...	Northwest slope, 2.5°	961	33–40	Mesic woodland herbs and shrubs (abundant)	9	8	17	9
13...	Northwest slope, 13°	1009	25–30	Lonicera dioica (abundant)	7	10	12	10
14...	Northeast slope, 4.5°	998	28–33	Mesic woodland herbs and shrubs (rare)	7	7	9	10
15...	South slope, 2.5°	972	29–35	P. quinquefolia (abundant)	10	10	21	4
16...	Southeast slope, 7°	951	30–35	Mesic woodland herbs and shrubs (rare)	8	9	14	4

broken in 1938. Its root system was the most massive of the three species. Typically deep rooted, it proportionately contributed a smaller amount of root area in the upper A_1, A_2, and B_1 than did the specimens of red oak and sugar maple studied. The red oak partially excavated was 97 years old, 22 inches in diameter at a height of 2 feet, and was also wind-broken in 1938. Its root system was less massive than that of the white oak but contributed heavily in both large and small roots to the upper three horizons. No large sugar maple was available for excavation, but a smaller specimen, wind-broken in 1940, was investigated. It consisted of two

sprouts, each 15 years old, and had a diameter of 4 and 3½ inches, respectively, at a height of 2 feet. The most marked character of the root system was the mass of smaller roots (< ¼ inch in diameter) which ramified throughout the upper three horizons (fig. 5). The relative number of deep anchorage roots was as great as in the red and white oaks. The response of maple seedlings to the effects of increased insolation following tree wind fall or wind break and subsequent canopy opening was also of interest (fig. 20).

Discussion

The significance of some of the findings has been treated in sections on soil factors and root data. On the whole, the results are in accord with those of previous investigators. Coile (3) examined four profiles in an uneven-aged stand of white oak–black oak–red oak on Georgeville stony clay in the Duke Forest, North Carolina. Korstian and Coile (9), in reporting the same study, state: "The most striking features are the relatively large number of small roots in the upper few inches of soil and the paucity of roots of the two smallest size classes (< 0.1 and 0.11 to 0.30 inch) in the B and C horizons." While this condition is also true at Wychwood for comparable size classes (table 2), the present profiles, regardless of type of trench employed, showed greater numbers of roots in all horizons than were encountered by Coile. The only profiles comparable with his in number of roots per horizonal square foot were those here investigated because of scarcity of herbaceous and woody ground cover (stations 1, 2, 3, 14, and 16). The differences in root numbers probably are due to the regional locations of the respective stands and to differences in soil types and amount of herbaceous ground cover.

The soil type at Wychwood, Bellefontaine silt loam, obviously is capable of allowing the development of comparatively large numbers of roots, particularly in the A_1 and A_2 horizons. In the B_1 horizon the roots were found to penetrate the soil in comparatively large numbers, not only along the sutures of the characteristic nut structure, but also—though less frequently—through the nutlets.

In accordance with earlier findings (16, 2, 10, 3, 13, and others), this study has shown a differential suitability for root development in the different horizons. The greater number and percentage cross sectional root area per square foot in the A_1 horizon was expected, for it is here that oxygen, water, and nutrient supplies are usually most favorable. The exception in stations 7 and 15, in which the A_2 surpasses the A_1 in numbers and root area, indicates that regardless of the potential suitability of a horizon for root development, the actual root distribution is conditioned by the type of root system of the dominant or subdominant species in the area. Further, root systems of such ground cover species as *Parthenocissus quinquefolia* will distort the results in any study where an attempt is made to measure only tree roots, unless great care is taken to identify each woody root encountered, particularly smaller ones. Especially is this true in deciduous forests, where

herb and shrub ground cover makes it almost impossible to obtain an accurate measure of tree roots only.

The concentration of root numbers and cross-sectional root area in the upper foot of the profiles suggests that aeration is possibly of significance. This point was further emphasized by the low number of smaller roots in lower levels of the profile. Correspondingly there were more dead roots in the lower depths. While such findings point to lack of aeration as a limiting factor for root development with increased depth, it is probably not the only factor involved. This view is substantiated in areas where the canopy has been opened through wind-break or wind-fall, where tree seedling and herbaceous root development is greater at all levels of the profile. Thus it is debatable whether the greater development of roots in the upper part of the soil is a response to more favorable aeration, moisture, or temperature conditions. These factors, as well as a more abundant supply of available nutrients and inherent tendencies of native species when grown under low light intensity, probably are interrelated in influencing the greater root development in the upper soil section.

Areas comparatively free of ground vegetation—for example, stations 1, 2, 3, 14 and 16—had fewer roots although they possessed a higher average cross-sectional area per root than did those stations with abundant ground cover, regardless of type. The findings in the former stations thus primarily indicate the root condition of the trees which make up the canopy. On the other hand, root numbers recorded for profiles of "bare" stations are in themselves comparatively large. An area with abundant ground cover was found (station 15) whose root numbers and area equaled that of a "bare" area. This suggests that the relative proportion of woody to herbaceous roots fluctuates throughout the forest. It is possible that the woody roots in bare areas may draw heavily upon the supplies of the soil environment and thereby limit the establishment of herbaceous species. Unpublished results of trenched quadrat studies, however, suggest that such root competition is not critical.

When stations 1 to 16 were sampled during the summer of 1938 by rectangular trenches, it seemed that the selected wall was not always typical of the root distribution on the four walls. This was particularly true in areas with abundant ground cover where several herbaceous or woody plants appeared near one or more of the walls. Because of this visible local heterogeneity in root distribution, it was decided to test the usefulness of square trenches—in which equal areas on all four walls are charted. Such sampling should diminish the influence of root systems which, with predominating numbers, approach the trench from one direction. Further, since the problem of sampling root distribution is basically statistical, the method should yield a more accurate measure of the distribution with respect to all directions, especially where undue directional effects are evident. In the square trenches the root data from the four walls may be totaled.

In table 7, the two walls of each trench varying the most with respect to the A_1 horizon are compared statistically as to root numbers. Results much more significant were obtained when horizon extremes of each trench were compared. However, since only one wall would have been selected in using a rectangular trench, the comparisons are on a wall-for-wall basis.

The probability of occurrence for differences between two walls of the same trench ranged from 1 chance in 100 (very significant) to 1 chance in 2 (no significance). In station 12, located on a 2.5° slope, the two walls showed significant differences in the upper four horizons. Stations 11, 13, 14, 15, and 16 had walls

TABLE 7

t TEST OF ROOT NUMBER MEAN DIFFERENCES BETWEEN WALLS OF SQUARE TRENCHES

Station	Walls	Horizon	$\bar{D}/S.E._{\bar{D}}$	Value of t	Station	Walls	Horizon	$\bar{D}/S.E._{\bar{D}}$	Value of t
11	N.W. vs. N.E.	A_1	517/157	3.292*	14	E. vs. W.	A_1	209/69	3.028*
		A_2	136/42	3.238*			A_2	44/13	3.384*
		B_1	45/36	1.250			B_1	64/36	1.777
		B_2	5/12	0.416			B_2	13/5	2.600
		C_1	24/8	3.000*			C_1	8/6	1.333
12	S.E. vs. N.E.	A_1	564/93	6.064†	15	E. vs. S.	A_1	126/45	2.800*
		A_2	337/85	3.964*			A_2	166/109	1.495
		B_1	122/15	8.133†			B_1	84/28	3.000*
		B_2	85/15	5.666*			B_2	3/4	0.750
		C_1	24/11	2.181			C_1	8/11	0.727
13	N.W. vs. S.E.	A_1	388/124	3.129*	16	S.E. vs. N.W.	A_1	240/67	3.583*
		A_2	144/42	3.427*			A_2	41/29	1.413
		B_1	6/9	0.666			B_1	59/33	1.484
		B_2	36/15	2.400			B_2	14/13	1.076
		C_1	8/6	1.333			C_1	10/4	2.500

* Significant at 5% level.
† Significant at 1% level.

whose horizonal differences in root numbers were significant in 1 to 3 of the total five horizons. Two rectangular trenches were tested similarly. Here each initial 6-foot section was divided into two sections 3 feet in length to afford a statistical basis for application of the *t* test. In each of these stations the two sections differed significantly only in the A_2 horizon. In these cases either the writer was fortunate in selecting walls which showed little variation or it is to be expected normally that, owing to directional effects, one wall will show less variability than that between any two walls of the same trench. It is possible that the remaining three walls of these rectangular trenches would have shown significant differences from the selected 6-foot walls.

The results from the two types of trenches have been reported together, but the square trenches were assigned more weight. Root numbers obtained from rec-

tangular trenches in bare areas were comparatively lower than those obtained from square trenches in similar areas. Numbers secured from the former trenches were probably not an accurate sample of the true root distribution. The same is true to varying degrees of other station types investigated by the two types of trenches; for example, station 7 vs. station 15, station 5 vs. station 11, etc. The results from square trenches were obviously most accurate when listed as a total of the four walls, yielding a sample 12 feet in length compared with 6 feet for the rectangular trench.

The use of square trenches affords a basis for statistical comparison of root numbers obtained in different station types within the same plant community.[4] Observation of the basic differences of root distribution within a community on one soil type speeds the determination of the significant relationships of the same community on several soil types. The comparison may be focused on horizons, profile sections, or total profiles. Analysis of horizonal differences in root numbers between the different station types was carried out for stations 11–16.

Significant horizonal differences were obtained for stations 11, 12, and 13, with good ground cover, as opposed to stations 14 and 16, with sparse cover. Further, there were no horizonal differences in root numbers among stations 11, 12, and 13, or among stations 14 and 16, except in the C_1 horizon in the latter stations.[5] Such local differences might be expected considering the heterogeneous distribution of the dominant tree species, with their differing types of root systems. On the other hand, station 15, with a dense society of *P. quinquefolia* as ground cover, differed in the same direction from stations 11, 12, and 13 as did bare stations 14 and 16. However, the A_2 horizon of station 15 significantly surpassed the A_2 of the two bare stations in root numbers and was equivalent in numbers to the others with abundant cover. If one assigns to the A_1 and A_2 horizons more importance than to the others, station 15 must be segregated as possessing a distinct type of root distribution. This is in accord with the distribution in the A_1 and A_2 of this station, which is conditioned by the type of root system of the dominant ground cover species and not by the apparent relative suitability of the respective horizons.

The root-volume results give further evidence of the heterogeneity of root distribution in the deciduous forest. They indicate that the upper 8 inches of the soil contain the largest volume of roots. Samples were not taken below the first foot, but it seems unlikely that greater volumes would be found at lower levels—unless exceptionally large tree roots were encountered. The amounts are approximately equal to those found by Weaver and Harmon (19) in the prairie.

[4] A standard error can be obtained for each trench, since each wall, by subdivision into 1-foot sections, can yield a mean observation.

[5] In the *t* test, "difference" is intended to mean only significant differences (those at or above the 5 per cent level in Fisher's probability table).

Earthworms, in mixing and penetrating all horizons, are obviously of benefit to the aeration, fertility, and water relations of the profiles. Such activity warrants further investigation. Cicada activity within the soil, while most vigorous during emergence of the nymphs, is favorable in providing drainage channels and in effecting better aeration, particularly of the B_2 horizon. Its effect is probably felt for a number of years in ungrazed forests.

Summary

1. The relationship of the Bellefontaine silt loam soil profile, with its inclusions, to the root development of the native species in the maple-oak forest at Wychwood, Lake Geneva, Wisconsin, was studied during the summers of 1938–1940. Stations were selected to obtain a cross-section of the varying conditions in the forest.

2. Sixteen station types were investigated by the trench method of root-distribution sampling. In six of the station types a new, square method of trenching afforded more accurate measurement of the heterogeneous root distribution than did the rectangular trenches most commonly employed.

3. Root systems of herbaceous and woody seedlings in the various station types were excavated and their relation to the upper horizons noted. Large specimens of sugar maple, red oak, and white oak also were partially excavated. Root volumes were obtained from surface cubic-foot samples in each station type. Cicada and earthworm activity was observed.

4. Greatest concentration of the smallest roots, 0.1–1.0 mm. in diameter, was in the A_1 horizon. Larger roots did not show an increase in numbers per unit horizon surface below the A horizons. Greater numbers of dead roots occurred in lower horizons.

5. On root number and percentage root-area basis, horizons A_1, A_2, B_1, B_2, and C_1 generally showed successive decrease in suitability for root development. On the same basis there were marked decreases, with two exceptions, of root numbers and area with successive 1-foot increases in depth to 3 feet.

6. Areas with sparse ground cover showed low root numbers and comparatively high percentage root areas. Stations with more abundant ground cover were characterized by larger root numbers and smaller percentage root areas.

7. Earthworm and cicada activities, particularly the former, were important factors in the soil environment. Such activities were more or less uniform throughout the woodland.

8. In all cubic-foot root-volume samples, the 0–8 inch level contained 80 per cent or more of the total root volume present in the sample. When the sample lacked roots $> \frac{1}{2}$ inch in diameter there were successive decreases in volume in passing into the 0–4, 4–8, and 8–12 inch levels.

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